CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 52 March, 1952

THE DISTRIBUTION PATTERNS OF THREE PLANT SPECIES IN AN OLD-FIELD COMMUNITY IN SOUTHEASTERN MICHIGAN

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Accepted for publication February 12, 1951

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INTRODUCTION

AS part of a long-term project to study the organization and operation of a natural community, we have recently published a preliminary description of the vegetation of an abandoned field on the Edwin S. George Reserve of the University of Michigan, Livingston County, southeastern Michigan (Evans and Cain, 1952). In this description attention was called to the mosaic or patchwork character of the community. The spatial organization and structure of a community are in part the result of the distribution patterns exhibited by its component species. In the majority of natural situations, regular or truly random distributions of individuals are rare. On the contrary, species populations generally show varying degrees of aggregation or clumping, of the type that has become known as "contagious" distribution. The result is that few communities are perfectly homogeneous throughout their extent, but present instead a series of patches which, in turn, have a distributional pattern of their own.

Knowledge of patterns of distribution is necessary, not only to the community ecologist, but also to the population geneticist, who wishes to describe the degree of isolation from other individuals and populations as well as the possibilities for exchange of genetic material through interbreeding. The description, in adequate quantitative as well as qualitative terms, of the patterns of distribution displayed by the various species and by the community as a whole presents a difficult and frustrating problem, but one whose solution is desirable if one is to have a clear picture of community structure.

Information about distribution patterns may be obtained by various sorts of sampling procedure. For example, recent studies by Archibald (1948) and Thomas (1949) have attempted to describe distribution in terms of the frequency of occurrence in quadrats of uniform size. By recording the number of individuals present in each quadrat, one obtains the number of quadrats with 0, 1, 2, or more individuals, and these data can then be tabulated as a frequency distribution. This procedure is considerably simpler and less laborious than mapping the exact location of every individual within the given population. The picture of the distribution which it produces, however, is a formalized one which conceals the true distribution pattern, for it fails to indicate the spatial relations within and between the quadrats from which the frequency data were derived. It is evident that the size of quadrat chosen for such sampling may have considerable effect upon the resulting distributional picture. In addition, since the exact distribution patterns are generally not available to the reader, it is impossible to evaluate the information obtained from the quadrat data; that is, it is impossible to determine the extent to which the synthetic picture conforms to reality.

We approached this problem by considering the distributional patterns of three plant species which are components of the old-field vegetation. The locations of individual plants were plotted on a map (Map 1), which was then subjected to analysis by means of quadrats (Figs. 1, 2, and 3). Although none of the three species was of major importance in the community, their size and conspicuousness, as well as the ease with which individuals could be distinguished, made them especially suitable for this study. Our interest lay more in the development of a satisfactory technique which might be applicable to other populations than in the particular patterns displayed by these species.

Acknowledgments

J. Speed Rogers, Director of the Edwin S. George Reserve, kindly made the facilities of the Reserve available to us for this study. The Cranbrook Institute of Science generously placed at our disposal both space and equipment to facilitate construction of the original map. Fernando Segadas-Vianna and Mrs. Emmy Hesz assisted us in the preparation of both map and charts. George W. Byers copied the map for publication. To all of these people and institutions we wish to express sincere thanks.

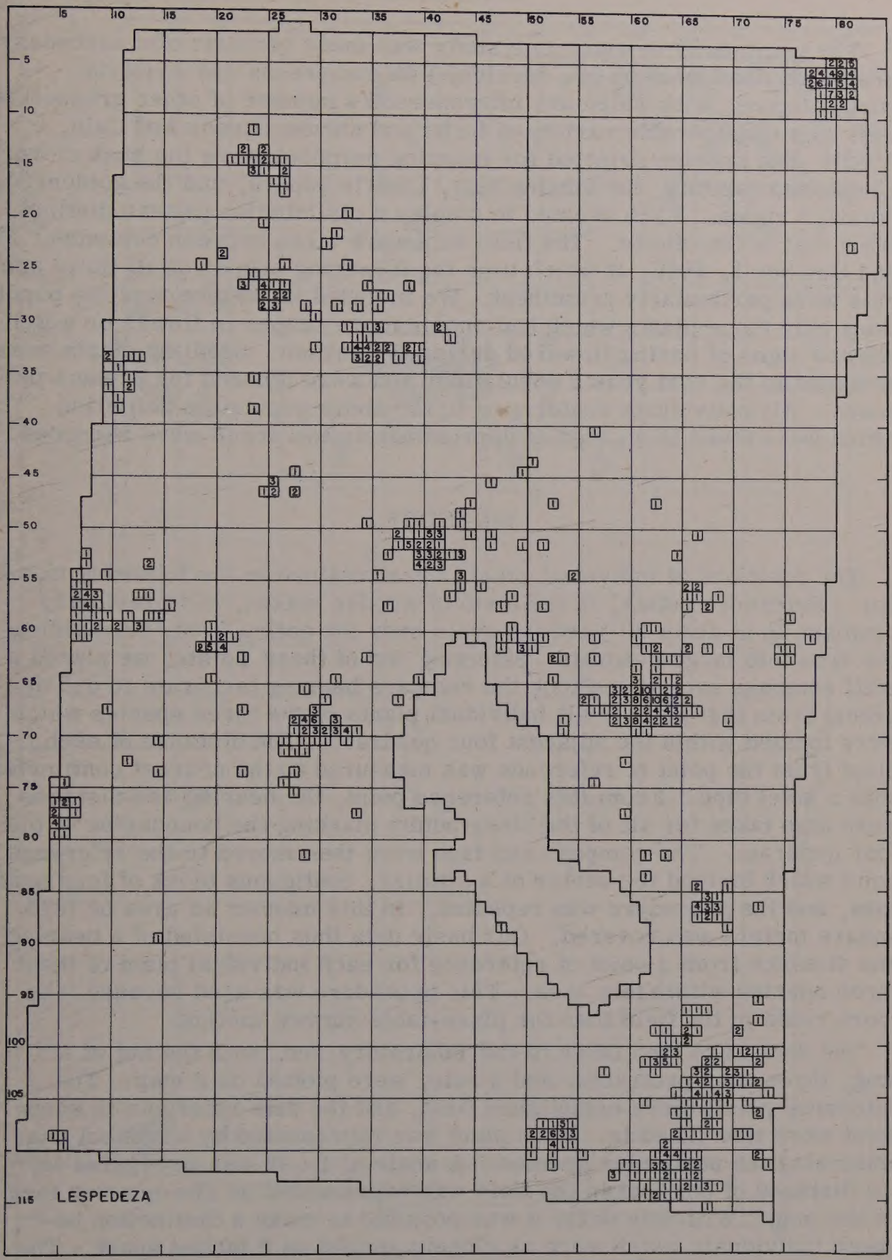


FIG. 1. Analysis of the Lespedeza capitata population given in Map 1, showing the numbers of individuals encountered in quadrats 1-meter square.

MATERIAL

The community in which this study was made consists of a secondary grassland dominated by two species, Poa compressa and Aristida purpurascens, with which are interspersed a number of other grasses as well as a considerable variety of forbs and shrubs (Evans and Cain, 1952). The species selected for mapping purposes were the bush clover, Lespedeza capitata, the blazing star, Liatris aspera, and the goldenrod, Solidago rigida. Each seemed to display a distribution pattern distinct from that of the others. The field data were taken between September 27 and October 3, 1949, at which time the flowering scapes of all three species were particularly prominent. We included as members of the populations only those plants which had one or more scapes in flower or which showed signs of having flowered during the season. Seedling plants were assigned to the next year's populations and were ignored for present purposes. All individuals conforming to the above population definition which were found in an area of approximately two acres were recorded.

METHODS

The positions of individual plants were obtained in the following manner. Reference points, in the form of wooden stakes, had previously been set up at about 20-yard intervals over the entire field, subdividing the area into large quadrats. Selecting one of these points, we placed a staff compass over it and took the compass bearing (accurate to 0.5 degrees) from that point to all individual plants of the three species which were located within the adjacent four quadrats. The distance of each plant from the point of reference was measured to the nearest centimeter with a steel tape. From this reference point, the bearing and distance were also taken for all of the other points marking the boundaries of the four quadrats. The compass and tape were then moved to the reference point which formed the center of a similar, contiguous block of four quadrats, and the procedure was repeated. In this manner an area of 7873 square meters was covered. Our basic data thus consisted of a bearing and distance from a point of reference for each individual plant of these three species within this area. This procedure was used because it is more rapid in the field than the plane-table survey method.

The data were then taken to the laboratory and, with the aid of a long, three-arm protractor and a rule, were plotted on a map. The reference points were established first, and the data referable to each point were then filled in. Each plant was represented by a symbol characterizing the particular species. A scale of 1 : 48 was used; that is, the distance of one foot in the field was represented as one-quarter inch on the map. With this scale it was possible to make a distinction between individuals which were as closely spaced as 6 inches apart. The entire map covered an area of about 5 by 7 feet and was made on pieces of heavy illustration board 30 by 40 inches each, so that smaller sections of the map could be examined separately. The whole map has been reproduced on a much smaller scale (Map 1).

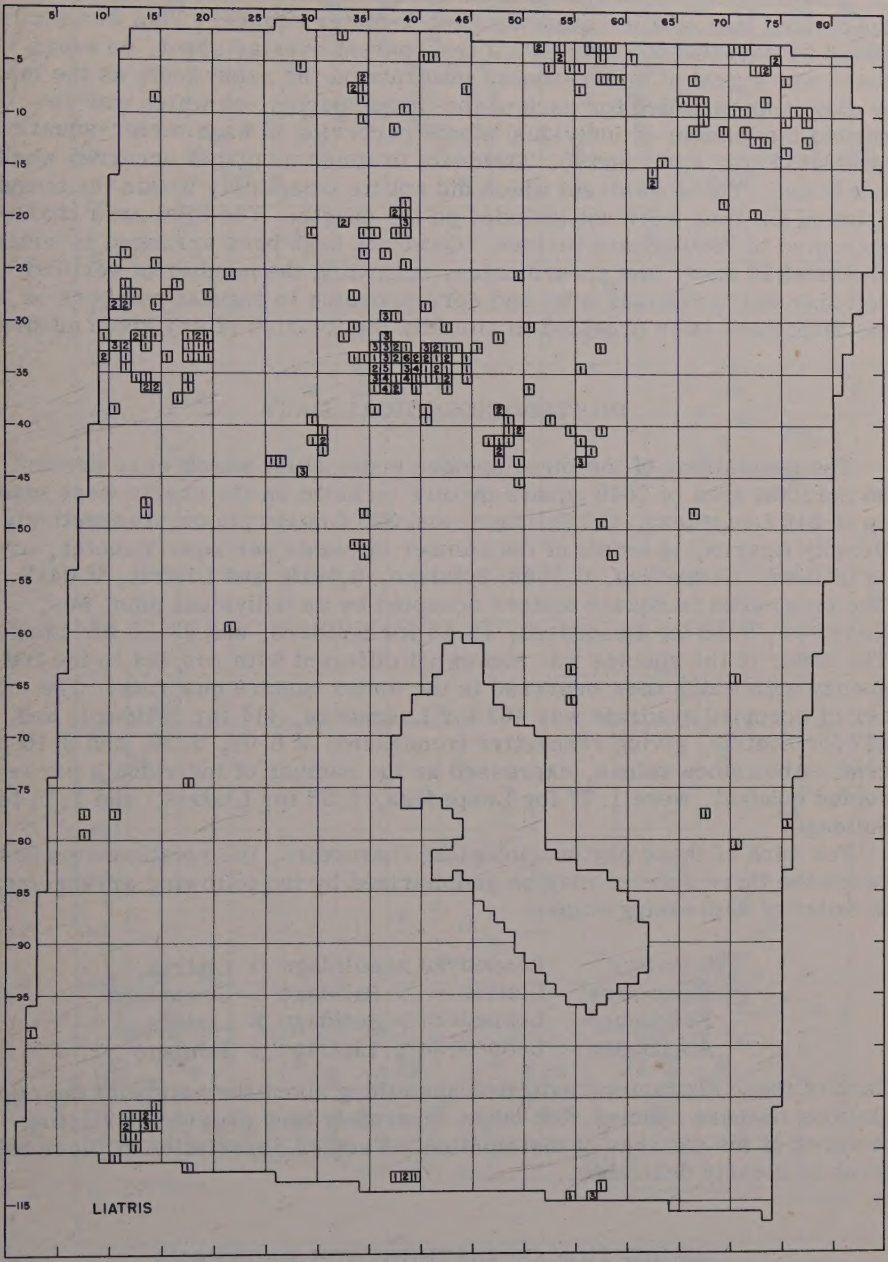


FIG. 2. Analysis of the Liatris aspera population given in Map 1, showing the numbers of individuals encountered in quadrats 1-meter square.

To analyze these distribution patterns, the entire mapped area was subdivided into smaller quadrats each 1-meter square. This was facilitated by covering the map with a transparent overlay sheet, on which there was a grid of meter-square quadrats on the same scale as the map. A chart was provided for each of the three species, on which was recorded the number of individual plants occurring in each meter-square quadrat (Figs. 1, 2, and 3). Quadrats in which no plants occurred were left blank. Those quadrats which did not lie completely within the boundaries of the map were not included on the charts. The total area charted amounted to 7640 square meters. Quadrats have been arranged in square blocks of 25 each, and co-ordinates, indicating the number of vertical columns and horizontal rows and corresponding to similar numbers on the map, have been provided to simplify the location of any given quadrat.

PHYTOSOCIOLOGICAL DATA

The populations of the three species under study which were present on the total area of 7640 square meters included on the charts were made up of 816 Lespedeza, 473 Solidago, and 320 Liatris plants, respectively. Density figures, in terms of the number of plants per square meter, are as follows: Lespedeza, 0.1068; Solidago, 0.0619; and Liatris, 0.0419. The mean area in square meters occupied by an individual plant was, therefore, 9.36 for Lespedeza, 16.15 for Solidago, and 23.88 for Liatris. The order of the species was somewhat different with respect to the frequency with which they occurred in the meter-square quadrats. The number of occupied quadrats was 462 for Lespedeza, 411 for Solidago, and 237 for Liatris, giving respective frequencies of 6.05, 5.38, and 3.10 per cent. Abundance values, expressed as the number of individuals per occupied quadrat, were 1.77 for Lespedeza, 1.35 for Liatris, and 1.15 for Solidago.

For each of these phytosociological characters, the relationships between the three species may be summarized by the following arrangement in order of decreasing values:

Density: Lespedeza > Solidago > Liatris
Mean area: Liatris > Solidago > Lespedeza
Frequency: Lespedeza > Solidago > Liatris
Abundance: Lespedeza > Liatris > Solidago

Each of these characters indicates something about the nature of the populations of these species, but taken separately they provide conflicting pictures of the patterns of distribution. Further description of these patterns is clearly desirable.

DESCRIPTION OF DISTRIBUTION PATTERNS

The tendency of the plants of these three species to occur as clumps is readily apparent. A considerable area in the lower center of the map and charts is seen to be altogether devoid of individuals. This area rep-

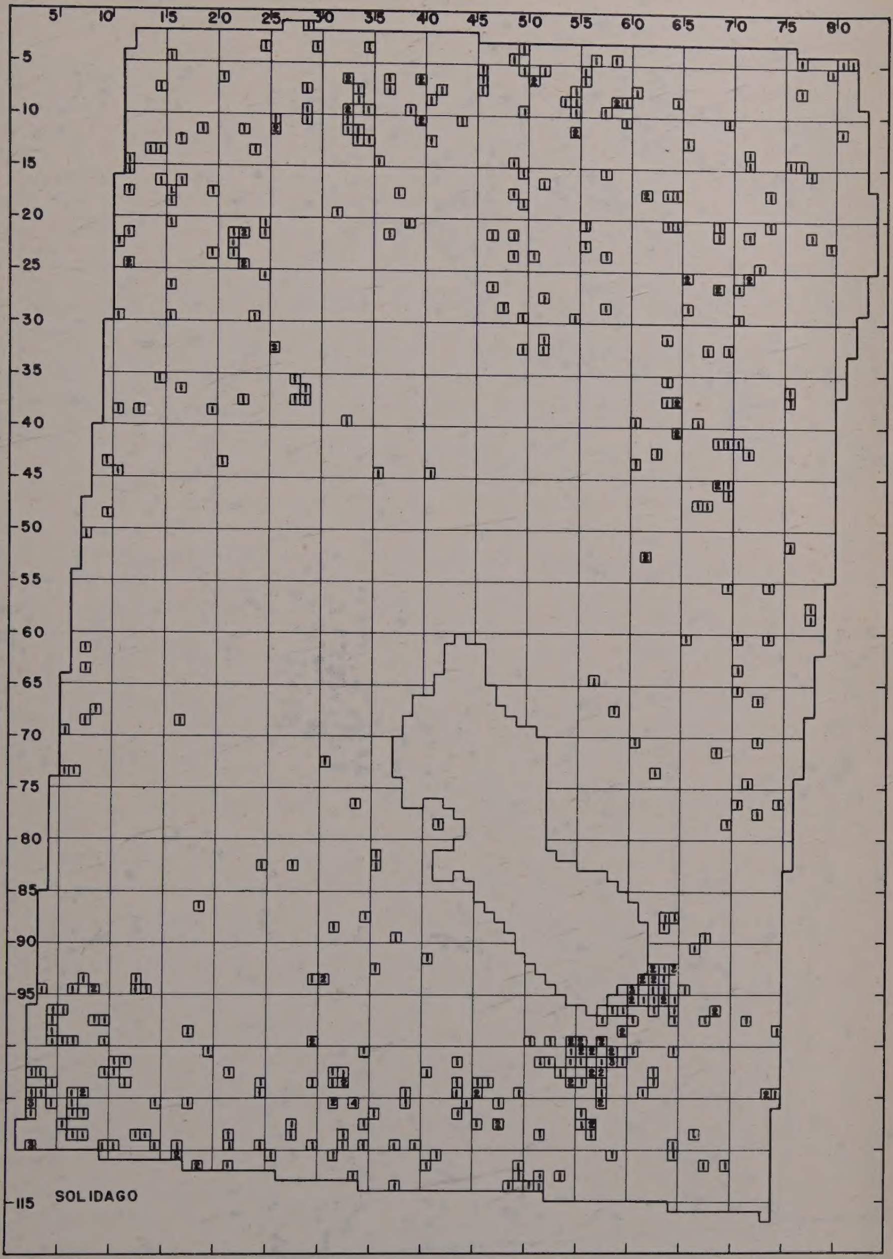
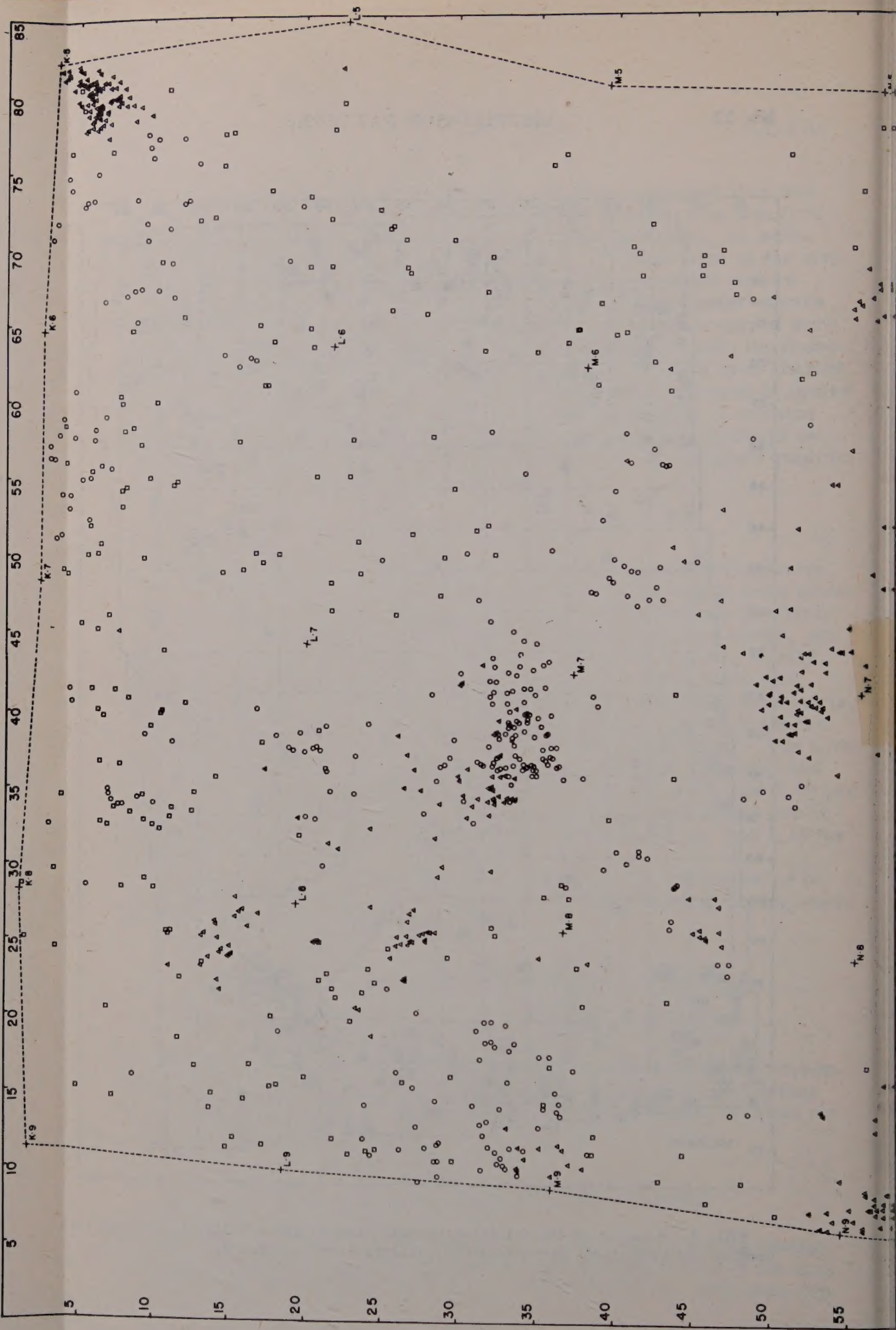
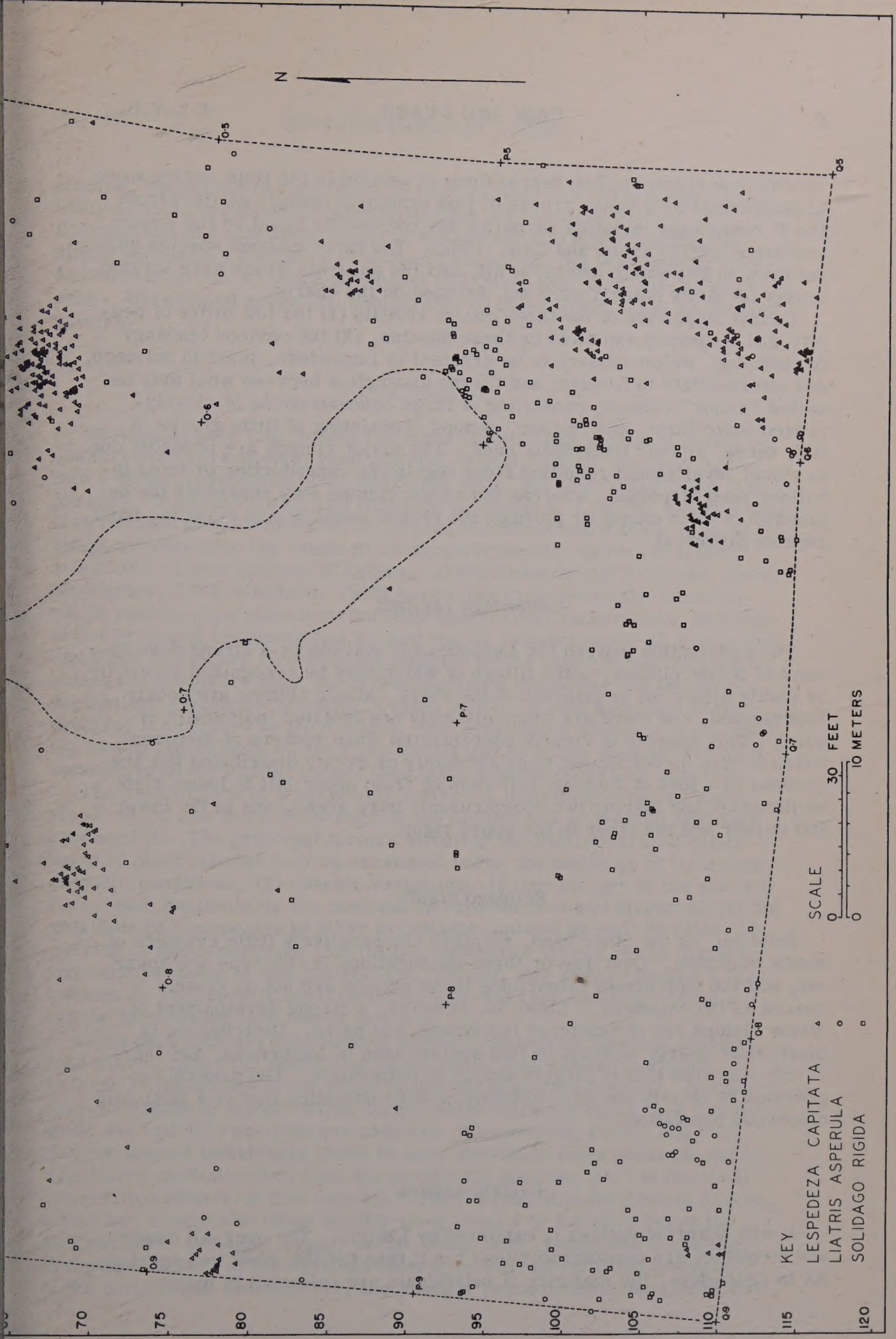


FIG. 3. Analysis of the Solidago rigida population given in Map 1, showing the numbers of individuals encountered in quadrats 1-meter square.



MAP 1. Locations of individual plants of Lespedeza capita
of a grassland community, Edwin S. George Reserve, Living
3, 1949.



is aspera, and Solidago rigida in approximately two acres
ty, Michigan, from field data taken September 27 - October

resents one of the shallow depressions or swales in the field, which were characterized by a dense growth of Poa pratensis sharply distinct from the P. compressa-Aristida purpurascens community found on the higher and drier levels (Evans and Cain, 1952). The three mapped species did not grow in this swale habitat at all, and the quadrats which were located wholly or partly therein were not included on the charts.

Casual inspection of the three charts reveals (1) the low order of density and frequency exhibited by these species, (2) the obvious tendency to clumping, which appears to be greatest in Lespedeza, least in Solidago, and intermediate in Liatris, and (3) the distinction between what may be called "major" clumps, consisting of large concentrations of closely-spaced individuals, and "minor" clumps, consisting of little groups of two, three, or four individuals each. The major clumps are probably due to clonal development resulting from vegetative reproduction or from localized seed dispersal, whereas the minor clumps may represent the beginnings of such clones or perhaps the chance associations resulting from random dispersal.

Lespedeza capitata

The distribution pattern for Lespedeza is marked by a strong development of major clumps, some fifteen of which may be recognized as wholly or partly within the boundaries of the chart. Minor clumps are poorly represented, and there are also relatively few isolated individuals or pairs. This species is clearly concentrated about centers of dispersal, which in turn do not appear to be randomly or evenly distributed but are grouped in a sort of diagonal belt running from upper left to lower right on the chart and leaving two conspicuously bare areas, one in the lower left corner and the other in the upper right.

Solidago rigida

Solidago, on the other hand, displays comparatively little evidence of major clumping. Only two or three aggregations of this type are apparent, and the individuals comprising these clumps are not as closely spaced as in Lespedeza. There is, however, a strong development of minor clumps and of scattered individuals and pairs. Distribution is much more nearly uniform in this species than in Lespedeza, and there is only one area that is largely devoid of individuals. The general impression is clearly one of a distribution approximating that of a randomly dispersed population.

Liatris aspera

A still different pattern is exhibited by Liatris. The over-all density and frequency are considerably less for it than for the other two species. As in Lespedeza, the majority of individuals are collected in major clumps, but not more than three or four of these are recognizable for Liatris, and the distances between clumps appear to be greater in Liatris than in Lespedeza. Liatris also shows more of a tendency to single individuals and pairs than does Lespedeza, but less than Solidago. Minor clumps are no more developed in Liatris than they are in Lespedeza. Unoccupied areas are comparable to those found in the Lespedeza pattern.

DISCUSSION

Ecologists have long sought for some satisfactory means of giving quantitative expression to such patterns of distribution, not only to obtain a better understanding of their structure, but also to facilitate comparison. Thomson (1952) has fitted the Lespedeza, Liatris, and Solidago distributions described above to several mathematical models in an attempt to determine the extent to which such models represent natural situations. Other authors (Clapham, 1936; Fracker and Brischle, 1944; McGinnies, 1934; Whitford, 1949) have tried to measure the extent to which certain population distributions depart from randomness, but none of the proposed measures has proved wholly reliable under all conditions, and their values are considerably affected by the size of quadrat used to obtain the frequency data, as is demonstrated elsewhere for the three populations discussed herewith (Evans, 1952). A new approach to the problem is provided by Dice (1952), who proposes a measure of the spacing among individuals within a population that is based upon the distance between adjacent plants, rather than upon data derived from quadrats.

The significance of a particular pattern of distribution can be understood only if one has a knowledge of the factors and processes that have produced it. The principal factors affecting the local distribution patterns of plant species may be subsumed under the headings of (1) microclimatic conditions, (2) edaphic variations, (3) the biology of the species concerned, particularly the methods of reproduction and dispersal, (4) the relations of the species to other organisms, animal as well as plant, occurring in the community, and (5) the element of chance in the dispersal and establishment of new individuals. Indeed, any description of a distributional pattern will itself be inadequate and lack meaning unless it can be interpreted in terms of process.

Lespedeza capitata possesses a slender, gradually tapering primary root which, under the conditions of the field, may extend to a depth of at least 36 inches and from which numerous branches develop. Excavation of Lespedeza plants having stems which were not more than 3 inches apart has failed to produce any evidence of connecting roots, and such closely-spaced individuals seem to have developed from separate seeds. Vegetative multiplication does not apparently play any part in the local distribution pattern of this species. This is true also for Liatris aspera, which has a cormlike tuber usually lying from 4 to 6 inches below the soil surface. Solidago rigida, on the other hand, possesses a shallow, creeping rhizome which develops lateral as well as terminal buds; as older parts of the rhizome die, the younger parts become separated and give rise to individual plants. It will be recalled that, although Solidago showed the least tendency toward major clumping, so far as these three species are concerned, it showed the greatest development of minor clumps, and it seems likely that this feature of its distribution pattern is largely due to rhizome spread.

There is also some evidence that the manner of seed dispersal has had its effect upon the patterns of distribution of these three species. The seeds of Lespedeza are heavier than those of Liatris or Solidago and, in contrast to these latter, are not equipped with a pappus for widespread aerial dispersal. Lespedeza seeds are therefore more likely to drop in the immediate vicinity of the parent plant. If a more limited seed distribution is actually the case with Lespedeza, this would help to explain the stronger tendency to major clumping displayed by this species. The closer approach to a random distribution demonstrated by Liatris and Solidago (Thomson, 1952) emphasizes the role that chance might be expected to play in the distribution of seeds by wind.

It would be premature at this point to try to evaluate the various factors responsible for these distributions. The complete absence of the three species from the swale habitat is suggestive of microclimatic and edaphic factors, or of competitive relationships to other plants, but further investigation of these aspects is required. More knowledge of the role of animals in the transportation of seeds is also needed. It is hoped that additional study of these and related factors will throw considerable light on the interpretation and significance of these patterns of distribution.

SUMMARY

The distribution patterns of populations of Lespedeza capitata, Liatris aspera, and Solidago rigida were obtained by taking the bearing and distance from a reference point of all individuals encountered in an area of approximately two acres. By means of these data, the location of each individual plant was plotted on a map. An overlay grid representing 1-meter-square quadrats was used to prepare frequency charts for the distribution of each species. Different relationships between the three species were indicated by the data for density, mean area, frequency, and abundance. The tendency to clumping appeared to be greatest in Lespedeza, least in Solidago, and intermediate in Liatris. A distinction was made between "major" clumps, which are probably due to clonal development resulting from localized seed dispersal or from vegetative reproduction, and "minor" clumps consisting of several individuals only, which may represent either the beginning of such clones or the chance associations resulting from random dispersal. The ability of Solidago to spread by rhizomes may account in part for the greater development of minor clumps in this species, while the possession of heavier seeds helps to explain the greater degree of major clumping in Lespedeza.

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